Trophic-Level Responses to Nutrient Treatment of Meromictic and Glacially Influenced Coghill Lake

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ABSTRACT: Prior to a 1990–1994 run decline, Coghill Lake consistently produced the highest single-system sockeye salmon *Oncorhynchus nerka* catches in Prince William Sound. Although limnological and juvenile fisheries data are not available before the run declined, we hypothesized that sockeye salmon fry produced from 3 consecutive years of high escapements (1980–1982) might have overgrazed the zooplankton forage base and reduced the lake's sockeye salmon rearing capacity. In 1993 the *Exxon Valdez* Oil Spill Trustee Council approved and helped fund a nutrient enrichment stock restoration project for Coghill Lake to mitigate the oil-damaged fishery resources. During 4 years of nutrient enrichment (1993–1996), the seasonal mean phosphorus concentration increased 22%, algal biomass of mainly genera edible by zooplankton increased 220%, and the standing stock (density) of the prevalent zooplankton (*Cyclops*) increased 117% compared to pre-enrichment years (1988–1992). The sockeye salmon population averaged 263,604 smolts before enrichment compared to 940,411 during treatment. This increased smolt production is attributed to increases in primary and secondary production because the number of smolts produced per spawner also increased during enrichment. The trophic-level responses to nutrient enrichment in meromictic, glacially influenced Coghill Lake were similar to those observed for other clearwater holomictic and meromictic lakes treated in Alaska.

INTRODUCTION

Historically, Coghill Lake produced the largest single-system sockeye salmon *Oncorhynchus nerka* catches within Prince William Sound (PWS), Alaska (Crawford and Simpson 1991). The highest run (catch and escapement) of 1.1 million sockeye salmon occurred in 1982, but between 1990 and 1994 the run averaged only 18,000. Several hypotheses have been proposed as causes for this decline. Edmundson et al. (1992) suggested it was caused by a decrease in zooplankton from excessive foraging by rearing sockeye salmon fry produced from the 1980–1982, 1985, and 1987 escapements that averaged 166,000, nearly 3 times the 30-year mean escapement. Top-down control by planktivorous fish and subsequent changes in fish production have been documented in other northern temperate (Carpenter et al. 1985) and subarctic Alaskan lakes (Kyle et al. 1988; Schmidt et al. 1994; Kyle 1996).

Other causes of the decline in the Coghill Lake runs have been considered. Willette et al. (1996) suggested the *Exxon Valdez* oil spill (EVOS) in 1989 may have exacerbated the decline in sockeye salmon production because juveniles may have suffered mortality during their migration through oil-contaminated waters in western PWS, although documented evidence was lacking. Also, climatic effects (e.g., temperature anomalies) on freshwater and marine survival could have contributed to the decline of the Coghill Lake sockeye salmon run. For example, Cooney et al. (1995) suggested subaverage sea-surface temperatures delayed pink salmon *O. gorbuscha* fry emigration in PWS; this placed fry in an unfavorable environment of less food resources, which apparently decreased fry survival. Although we recognize the importance of broad-scale temperature or energy variables to lake productivity (Brylinsky and Mann 1973; Nalewajko and Voltolina 1986; France 1992) and salmonid production (Plante and Downing 1993; Hinch

et al. 1995), there are no data to demonstrate that climatic changes effected the decline in Coghill Lake sockeye salmon runs. Although cause(s) for the decline in Coghill Lake sockeye salmon are speculative, pre-enrichment limnological sampling revealed that the lake was nutrient-poor and supported a relatively low standing stock (biomass) of phytoplankton and zooplankton (Edmundson et al. 1992).

Nutrient enrichment can increase a lake's rearing capacity by increasing the zooplankton forage base and hence sockeye salmon smolt biomass, which eventually produces greater adult returns (LeBrasseur et al. 1978; Stockner and Hyatt 1984; Stockner and Shortreed 1985; Kyle 1994a; Stockner and MacIsaac 1996; Kyle et al. 1997). The plan to restore Coghill Lake sockeye salmon included (1) nutrient treatment to increase productivity, and (2) changing management (PWSAC 1995) to obtain spawner escapements of 25,000, as derived from stock-recruitment and forage-base analyses.

Coghill Lake is meromictic; that is, the water column does not undergo complete circulation because of the presence of a dense water mass known as a monimolimnion. This anaerobic water mass prevents metabolites, derived from decomposing organic matter, from recirculating into the overlying oxygenated layers, or mixolimnion. Even during vernal and autumnal overturn nutrients remain unavailable to the mixolimnion (Wetzel 1975).

The proposal to treat Coghill Lake with nutrients raised a concern that the lake's meromictic nature could restrain fertilization benefits by limiting nutrient recycling. However, 2 other meromictic lakes in Alaska that were treated with nutrients produced positive results: (1) in Redoubt Lake, near Sitka, increases in secondary production effected larger smolts and higher adult returns (Kyle et al. 1997); and (2) in Hugh Smith Lake, near Ketchikan, increased secondary production produced more smolts, although smolt size was not affected (Peltz and Koenings 1989). Because Coghill Lake is glacially influenced, we wondered if the elevated glacial turbidity would counteract primary production through decreased light penetration (Koenings et al. 1986; Lloyd et al. 1987). Nutrient enrichment, however, was found to increase productivity in glacially turbid Kitlope Lake in British Columbia (Stockner 1987).

In 1993 the EVOS Trustee Council approved and partially funded a stock-restoration project for Coghill Lake. As mitigation for oil-damaged fishery resources, the Alaska Department of Fish and Game (ADF&G), in cooperation with the United States Forest Service,

were to conduct a 4-year nutrient enrichment project between 1993 and 1996. This paper assesses trophic-level responses to nutrient enrichment by comparing limnological and juvenile fish data before (1988–1992) and during (1993–1996) fertilizer treatment.

METHODS

Trade names mentioned in this section were included for scientific completeness and do not constitute endorsement by ADF&G.

Study Site Description

At an elevation of 18 m, Coghill Lake (61°4'N, 147°54'W) is located about 130 km northwest of Cordova, has a surface area of 12.7 km^2, a mean depth of 46 m, and a total volume of 587 x 10^6 m^3 (Figure 1). Its monimolimnion starts at about 30 m and composes approximately 45% of the total lake volume. A watershed area of 128 km^2, combined with a high precipitation (mean annual 330 cm) of the coastal region, produces a large annual runoff to Coghill Lake. Much of this runoff occurs in the form of silt-laden meltwaters from several surrounding glaciers, which impart seasonally variable turbidity. Coghill Lake is a fast-flushing system, the estimated annual water retention being 0.9 years. To supplement production, sockeye salmon fingerlings were planted in the fall: 330,000 in 1994 and 865,000 in 1995. However, in both years lake stocking occurred in early November. This is near the end of the growing season, which minimized competition with wild fry for food resources and prevented overgrazing of the forage base.

Nutrient Enrichment

Annual supplemental phosphorus (P) loading rates were estimated using procedures in Vollenweider (1976). An aqueous-blended P and nitrogen (N) fertilizer (20-5-0) and a N fertilizer (32-0-0) were sprayed over Coghill Lake from a fixed-wing aircraft. The fertilizer was applied on a weekly basis to the 5.5-km^2 middle third of the lake. During the 4 years of enrichment, annual fertilizer applications ranged from 363 to 1,287 kg of P and 2,125 to 8,014 kg of N (Table 1). The nutrient loading objective was to elevate the annual P concentration to benefit successive trophic levels without changing the oligotrophic status of the lake. The N fertilizer was added from late June or early July to mid or late August to counteract a summer

depletion of inorganic N (nitrate). N:P ratios >18:1 were maintained to discourage the growth of colonial nitrogen-fixing cyanobacteria (blue-green algae).

Limnological Sampling

Limnological surveys were conducted in 1986 at one sample site, Station A (Figure 1), and in years thereafter at Stations A and B, except in 1987 when there were no surveys. Surveys were conducted 4 to 8 times

each year between late June to early October. To better assess fertilization effects, Station C, located between Stations A and B in the lake fertilization zone, was established in 1993, the first year of nutrient treatment, to better assess fertilization effects.

Vertical profiles of temperature and dissolved oxygen were obtained using a YSI model 57 analyzer. Measurements of underwater light intensity, obtained using an International Light submarine photometer, were used to determine vertical light-extinction coef-
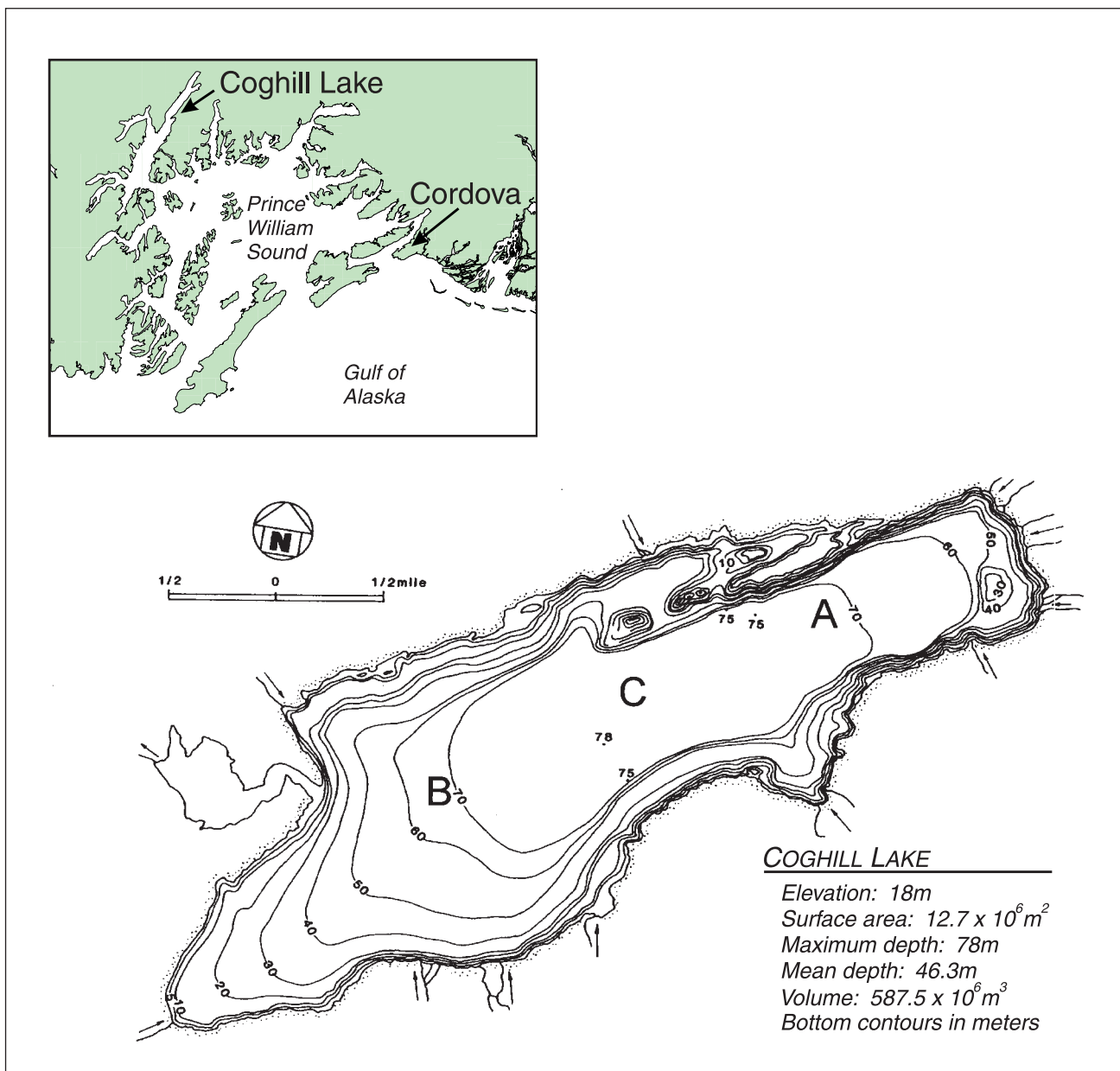

Figure 1. Geographical location and morphometrics of Coghill Lake in Prince William Sound, and location of sample stations (A, B, and C).

Table 1. Fertilizer application periods, types, and amounts of phosphorus and nitrogen applied to Coghill Lake, 1993–1996.

Application Period	Year	Amount (gal)		Amount (kg)	
		20-5-0	32-0-0	P	N
Jul 1–Aug 27	1993	3,520	4,978	363	8,014
Jun 23–Aug 13	1994	10,340	1,320	1,065	2,125
Jul 1–Aug 18	1995	13,704	1,875	1,412	3,019
Jul 1–Aug 26	1996	12,500	1,800	1,287	2,900
	Total	40,064	9,973	4,127	16,058

ficients (K_d) and compensation depths (1% of the subsurface intensity; see Kirk 1994). Water clarity was measured with a standard 20-cm black-and-white Secchi disk.

Turbidity was measured with a HF DRT1000 turbidimeter and expressed in nephelometric turbidity units (NTU). Color was determined on a filtered sample by measuring the spectrophotometric absorbance at 400 nm and converting to platinum-cobalt (Pt) units.

At each station water was collected from the 1-m stratum and at various deeper depths: in 1986 at 60 m; during 1988–1991 at 25 m; during 1992–1994 at 10, 20 and 30 m; and during 1995–1996 at 20 m. For each depth sampled, an 8-L water sample was collected using a Van Dorn sampler. Samples for dissolved nutrients (nitrate, ammonia, and reactive phosphorus) were filtered through a GFF filter within 12 h of collection. Total N and P concentrations were determined on unfiltered samples. All samples were analyzed at the ADF&G Limnology Laboratory in Soldotna, Alaska, using procedures described by Koenings et al. (1987).

Phytoplankton and Zooplankton Sampling

Algal biomass as indexed by chlorophyll-*a* concentration was estimated using the fluorometric procedure of Strickland and Parsons (1972). The low-strength acid-addition method recommended by Reimann (1978) was used to estimate phaeophytin. We filtered 1–2 L of sampled water through a 4.25-cm GFF filter to which we added about 2 mL of a saturated $MgCO_3$ solution just before we completed filtration. One 125-mL sample from the 2-m stratum was collected on each sample date, preserved in a Lugols acetate solution, and shipped to Eco-Logic, Ltd., of British Columbia, Canada, for phytoplankton identification and estimates of cell density.

Zooplankton tows were pulled vertically at 0.5 m·sec^{-1} from 25 m to the surface using a 0.2- or 0.5-m-diameter, conical net with 153-μm mesh. Zooplankton were preserved in 250-mL polyethylene bottles containing a 10% neutralized formalin solution (Haney and Hall 1973). Cladocerans and copepods were identified using the taxonomic keys of Brooks (1957), Pennak (1978), Wilson (1959), and Yeatman (1959). To enumerate, zooplankters in triplicate samples taken with a 1-mL Hansen-Stempel pipette were counted using a 1-mL Sedgewick-Rafter counting chamber. Zooplankter body lengths were measured to the nearest 0.01 mm for at least 10 individuals found along a transect in each of the 1-mL subsamples (Koenings et al. 1987). Zooplankton biomass was then estimated from species-specific regression equations derived from zooplankter body length and weight (Koenings et al. 1987).

Smolt Sampling

We used 3 inclined-plane traps (Todd 1994) to estimate the population of sockeye salmon smolts emigrating from Coghill Lake and to collect smolt size and age information. Trap efficiencies were estimated by marking smolts with a Bismarck Brown dye. Dyed smolts were released at an upstream site after assessing handling mortality and were subsequently recaptured in the traps, enumerated, and released. Trap efficiency trials were conducted approximately weekly, and the results were used to estimate smolt abundance for each trial period. We used Chapman's (1951) modification of the Peterson mark-recapture estimate following methods described by Seber (1982). In 1993–1995 trap captures were counted prior to marking; therefore, the estimate was for the unmarked population. In 1996 the composition of hatchery and wild smolts was estimated by scale patterns. Total smolt abundance and variance were es-

Table 2. Results of ANOVA using a randomized block design to test for significant differences ($\alpha = 0.05$) of mean values (at 1 m) for selected water chemistry parameters, nutrients, and algal biomass between Stations A and B (1988–1996), and between the pre-enrichment (PE; 1988–1992) and enrichment (E; 1993–1996) periods.

Variable	Units	Station mean		Approximate Probabilities	Period mean		Approximate Probabilities
		A	B	A vs B	PE	E	PE vs E
Water chemistry							
Conductivity	(μmhos·cm^{-1})	74	74	0.943	75	73	0.011
pH	(Units)	7.1	7.2	0.168	7.2	7.1	<0.001
Alkalinity	(mg·L^{-1})	19	20	0.364	20	19	0.002
Turbidity	(NTU)	4.9	4.5	0.228	4.6	4.8	0.067
Color	(Pt Units)	6.4	6.3	0.740	7.2	5.0	<0.001
Calcium	(mg·L^{-1})	7.5	7.4	0.794	7.7	7.3	0.096
Magnesium	(mg·L^{-1})	1.3	1.4	0.211	1.4	1.3	0.153
Iron	(μg·L^{-1})	221	180	0.076	214	180	0.012
Nutrients							
Total P[a]	(μg·L^{-1})	9.6	7.9	0.002	8.0	9.8	0.031
Total Filterable P	(μg·L^{-1})	3.5	3.9	0.581	3.7	3.8	0.003
Filterable Reactive P	(μg·L^{-1})	2.1	2.4	0.426	2.4	2.1	0.006
Total Kjeldahl N	(μg·L^{-1})	71	58	0.009	47	91	<0.001
Ammonia	(μg·L^{-1})	3.6	2.55	0.054	3.0	3.1	0.368
Nitrate + Nitrite	(μg·L^{-1})	19.4	13.9	0.038	18.8	13.4	0.010
Reactive Silicon	(μg·L^{-1})	645	626	0.163	726	499	<0.001
Algal biomass							
Chlorophyll-*a*	(μg·L^{-1})	1.18	1.23	0.765	0.64	2.05	<0.001

[a] Uncorrected for turbidity.

timated by summing the weekly estimates. During the trapping operation all smolts were individually enumerated, and a random sample of 20–40 smolts·d^{-1} were collected for age, weight, and length information. Stratified random sampling methods (Cochran 1977; Scheaffer et al. 1986) were used to estimate age-class proportions, mean lengths and weights, and variances. Daily strata were established and stratum weights were based on smolt abundance estimates.

Data Analysis

The effect of nutrient enrichment on general water chemistry, nutrient concentration, algal biomass (chlorophyll-*a*), and zooplankton abundance and biomass were assessed using analysis of variance (ANOVA) to test for differences between stations and between pre-enrichment and enrichment years. These analyses were conducted using a randomized, complete-block design (Neter et al. 1990). Because only Station A was sampled in 1986, this year was excluded from the statistical analyses; because Station C was not sampled before nutrient treatment, it too was excluded from the analyses. Potential seasonal differences among years were assessed by test-

ing for an interaction between season and year. This analysis was accomplished using a split-block design and defining year as the whole unit and season as the subunit. A density-weighted least-squares smoothing procedure was used to fit turbidity data against depth and lake area, and a 4th-order polynomial was used to plot seasonal changes in near-surface (1 m) temperatures as a function of time. All tests were conducted at $\alpha = 0.05$, and statistical analyses were facilitated using SYSTAT version 6 (SPSS 1996) or SAS/STAT version 6 (SAS Institute 1990).

RESULTS

Physical and Chemical Limnology

Inorganic turbidity from glacial meltwater is the major factor controlling light penetration in Coghill Lake. Turbidity was generally lowest in the spring and highest in the fall, which coincides with maximum rainfall and glacier melt. During 1988–1996, July–October mean turbidity in the 1-m stratum ranged from 2 to 10 NTU and averaged 5 NTU. We found no significant difference in turbidity for the 1-m stratum between
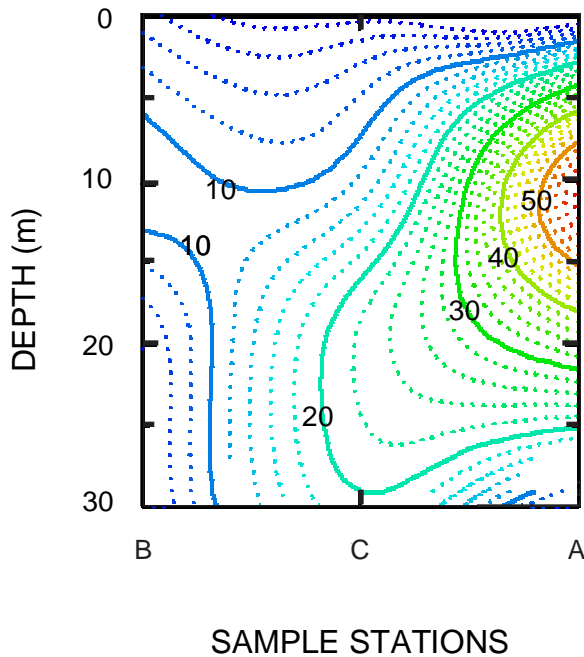
Figure 2. Contour plot of turbidity (NTU) in Coghill Lake, by depth and sample station, showing the extent of a glacier-induced turbidity plume for August 1993.

light is not always constant throughout the water column in Coghill Lake. For example, in September 1996 K_d was very high (3.34·m^{-1}) at the surface (1 m) near the major glacial inflow (Station A) but much lower (1.26·m^{-1}) at 3 m. In contrast, at Station B (furthest from the glacial inflow) K_d was lowest at the surface (0.37·m^{-1}) and higher (1.06·m^{-1}) at 3 m. The vertical changes in K_d reflect the horizontal and vertical turbidity gradients caused by the sporadic presence of glacial meltwater plumes and interflows.
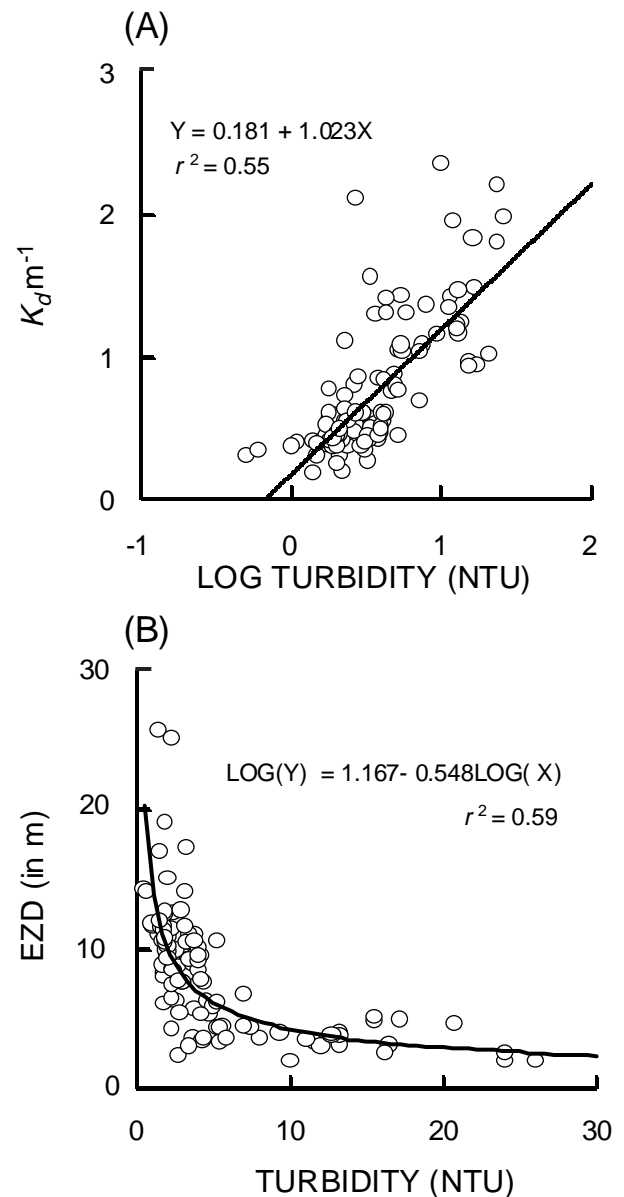

Stations A and B ($P = 0.228$), nor between the pre-enrichment and enrichment ($P = 0.067$) periods (Table 2). At times a strong, vertical turbidity gradient in Coghill Lake was evident. For example, in August 1993 surface (1 m) turbidity nearest the glacial inflow (Station A) was only 5 NTU, but at 10 m the turbidity, at 63 NTU was very high (Figure 2). Turbidity decreased at deeper depths and measured only 3 NTU at 30 m. Toward the opposite end of the lake (Station B), turbidity was more consistent across depths (6–12 NTU). In the middle of the lake (Station C) surface turbidity, at 4 NTU, was similar to that at Station B, but maximum turbidity, at 23 NTU, occurred at 20 m. Although the surface turbidity levels did not differ significantly between stations, the glacial meltwater entering Coghill Lake appears to gradually sink, causing turbidity to vary by depth and area.

Turbidity accounted for much of the variation ($r^2 = 0.55$) in the vertical light-extinction coefficient (K_d) in Coghill Lake (Figure 3A), and correspondingly the euphotic zone depth (EZD) was inversely related to turbidity (Figure 3B). During the 9 years sampled, we found no significant difference ($P = 0.390$) in EZD between Station A (mean 8.7 m) and Station B (mean 9.0 m); however, the EZD was shallower ($P < 0.0001$) during enrichment (mean 7.9 m) compared to pre-enrichment (mean 9.6 m). In addition, the diminution of

Figure 3. Relationship in Coghill Lake between (A) turbidity and the vertical light-extinction coefficient (K_d), and (B) turbidity and euphotic zone depth (EZD).

Coghill Lake ice breakup usually occurs in mid June; however, in some years the lake does not become ice-free until early July. Maximum surface temperatures ranged from 12° to 17°C, which occurred in late July or early August, and by October the mixolimnion was usually isothermic at 4°C. The growing season (when temperatures exceed 4°C in the 1-m stratum) averages a relatively short 148 d per year (Figure 4). Thermal stratification of the mixolimnion is weak because temperatures in late July and August decrease at $<1°C·m^{-1}$. Typically, temperatures cooled to about 4–5°C at the bottom of the mixolimnion in the summer. The input of glacial meltwater affects the thermal structure of Coghill Lake because the 1-m water temperatures nearest the glacial meltwater input (Station A) were often 0.5–1.0°C cooler than at the opposite end of the lake (Station B). However, temperatures at deeper depths were usually 1–2° C cooler at Station B than at Station A. The input and subsequent sinking of cold glacial meltwater creating interflows in this lake apparently contribute to complex vertical and horizontal temperature gradients that may influence biological productivity.

Vertical profiles of temperature, conductivity, and dissolved oxygen confirm that Coghill Lake is meromictic and has a monimolimnion beginning at about 30 m (Figure 5). Temperature and oxygen profiles in Coghill Lake show that the whole water col-

umn does not undergo complete circulation. Within the monimolimnion, temperatures remain relatively unchanged at about 6°C throughout the entire year (Figure 5A). The mixolimnion is separated from the dense monimolimnion by a steep (salt) concentration gradient or chemocline at between 20 and 30 m. Conductivity increased rapidly within the chemocline and reached 30,000 μmhos·cm^{-1} in the monimolimnion (Figure 5B). The calcium-to-magnesium ratio (by atoms) in the monimolimnion was about 27:1, which is close to the average ratio found in seawater (20:1). During most of the year, dissolved oxygen concentrations in the upper 20 m were usually around 100% saturation; however, below 30 m dissolved oxygen concentrations were $<3\%$ saturation (Figure 5C). During spring mixing, oxygen is replenished to some extent (50% saturation) only within the upper 10 m of the monimolimnion, or between 30 and 40 m. Thus, the high salt content and persistent lack of dissolved oxygen below 30 m indicate the monimolimnion is perennially stagnate.

Trophic Responses to Nutrient Enrichment

Although there were significant ($P < 0.05$) differences in mean concentrations of water chemistry measurements during pre-enrichment and enrichment (Table 2), most of the differences were small enough (1–2 units) to have no practical biological meaning. No differences in these parameters were found between Stations A and B. However, the May–October mean total phosphorus (TP) concentration (9.8 μg·L^{-1}) was significantly higher ($P = 0.031$) during enrichment, compared to pre-enrichment (8.0 μg·L^{-1}), and represented a 22% increase (Table 2). Filterable reactive phosphorus concentration, or the inorganic form of P that can be readily assimilated by phytoplankton, was low and at 2.3 μg·L^{-1} averaged about the same during pre-enrichment and enrichment, indicating that P in this system is in high demand. The annual input of TP to Coghill Lake from the watershed, fish carcasses, and fertilizer additions varied considerably (Figure 6). P from the fertilizer ranged from 28 to 110 mg·m^{-2}, which represented 30–50% of the total annual input during 1993–1996. In comparison, P from carcasses during the 4 years of fertilization accounted for only 3–10% of the total P input. The mean total Kjeldahl nitrogen (TKN) concentration nearly doubled during enrichment from 47 to 91 μg·L^{-1} (Table 2). In contrast, both nitrate and reactive silicon levels decreased by 30% during the enrichment period. Nitrogen to phosphorus (N:P) ratios in the mixolimnion
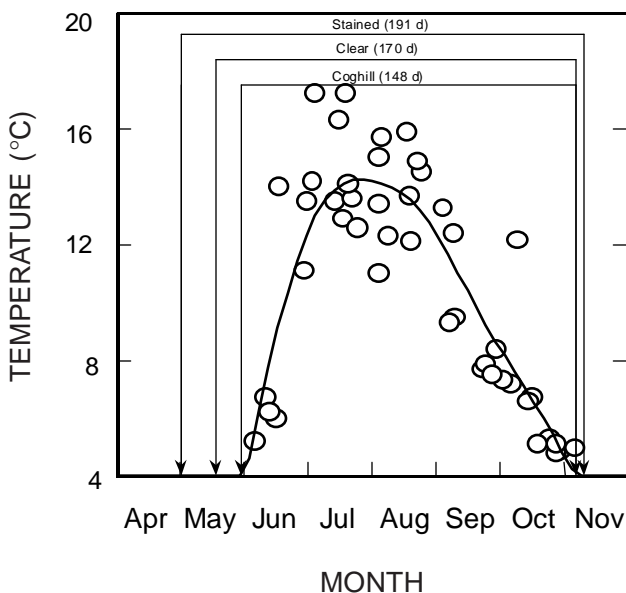

Figure 4. Growing season mean temperature curve at 1 m for Coghill Lake (1988–1996), and mean growing season duration and timing in Coghill Lake compared to Alaskan clear and stained lakes.
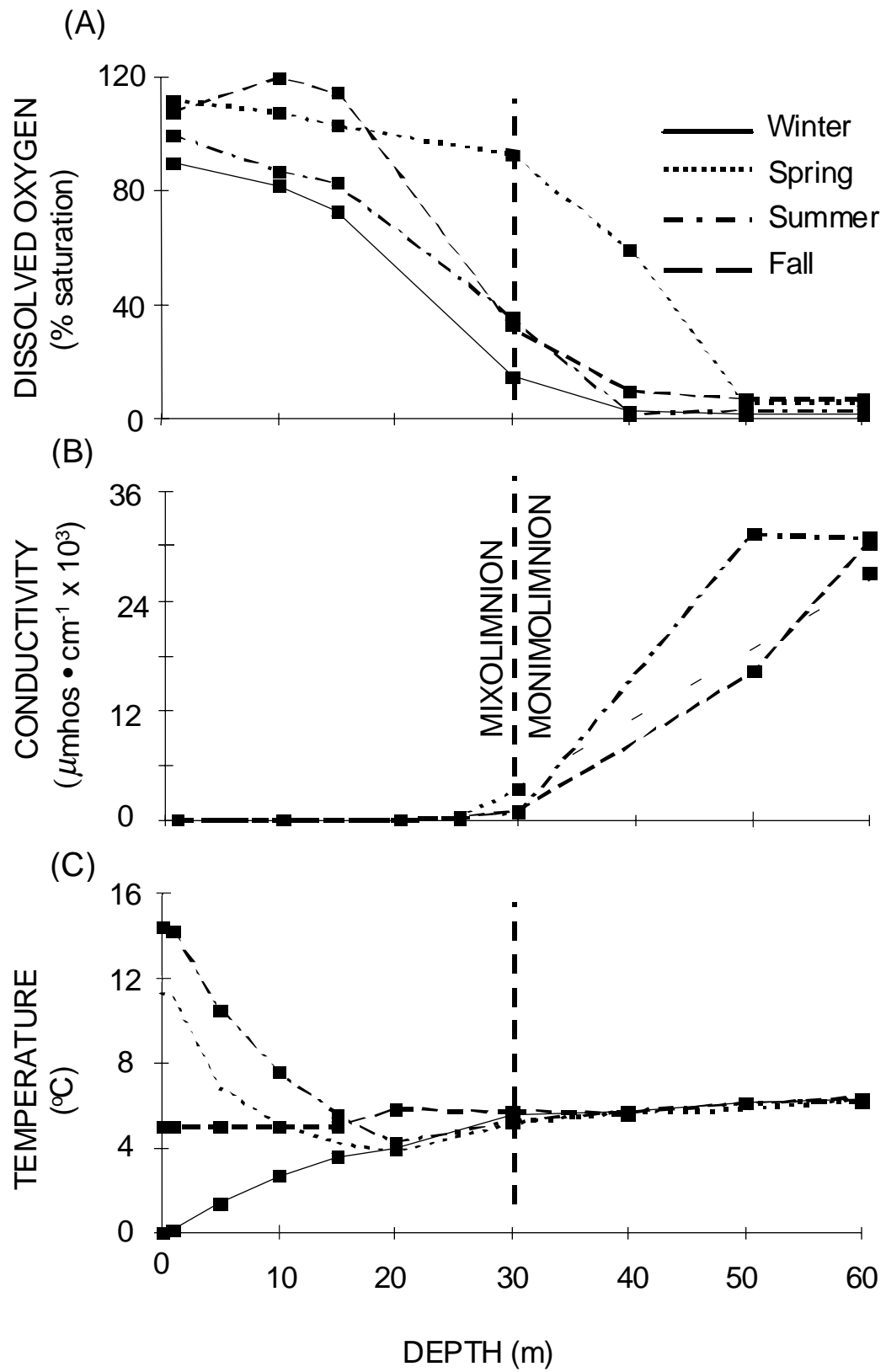
Figure 5. Vertical profiles of (A) dissolved oxygen, (B) conductivity, and (C) temperature in Coghill Lake across mixolimnion and monimolimnion.

ranged from 26:1 to 56:1 (by atom weight), but N:P ratios did not differ significantly following nutrient enrichment ($P = 0.430$). Finally, algal biomass (chlorophyll-*a*) in the mixolimnion of Coghill Lake increased 220% from a mean of 0.64 μg·L^{-1} during pre-enrichment to 2.05 μg·L^{-1} during enrichment (Table 2).

Because application of the fertilizer took place primarily during July and August, we questioned whether the differences in annual means detected by ANOVA (Table 2) correctly represented fertilization effects. For example, the difference in annual means in nutrient concentrations may have been more influenced by the spring or fall concentrations rather than by the summer concentrations, when the fertilizer was applied. Thus, we examined spring, summer, and fall means for selected limnological variables by year (Figure 7).

Spring and summer turbidity levels were relatively low (<5 NTU) and consistent during the pre-enrichment and enrichment periods; however, in the fall, turbidity dramatically increased to >5 NTU during both periods (Figure 7A). Spring TP concentrations were generally lower (<5 μg·L^{-1}) before enrichment than during enrichment (Figure 7B). In contrast, the mean TP concentration during the summer increased nearly 2-fold during enrichment to 11.2 μg·L^{-1} compared to

5.8 μg·L^{-1} during pre-enrichment. Fall TP concentrations did not increase significantly and followed the same trend as that for turbidity because of the peak input of glacial meltwater in the fall and the associated particulate P found in glacial silt. Reactive silicon was highest during the spring and lowest during the summer, and a trend of decreasing concentrations from spring through fall occurred during enrichment (Figure 7C). Nitrate concentrations showed complete inorganic N depletion during the summer (Figure 7D); concentrations remained at or near the analytical detection limit of <4 μg·L^{-1}. Both spring and fall nitrate levels decreased over the 9 years of sampling. TKN concentrations before enrichment were relatively consistent, but summer concentrations during enrichment were twice that of pre-enrichment levels (Figure 7E). We attributed the major increase in annual mean chlorophyll-*a* concentrations primarily to higher summer concentrations and secondarily to higher fall concentrations (Figure 7F). The higher chlorophyll-*a* levels during enrichment were not restricted to the surface of the mixolimnion; i.e., concentrations in excess of 2 μg·L^{-1} were found at 10 m in July and August when the fertilizer was applied.

Chrysophycean and cryptophycean flagellates 2–20 μm in size were the most common nanoplankton in Coghill Lake. Although the combined densities of ed-
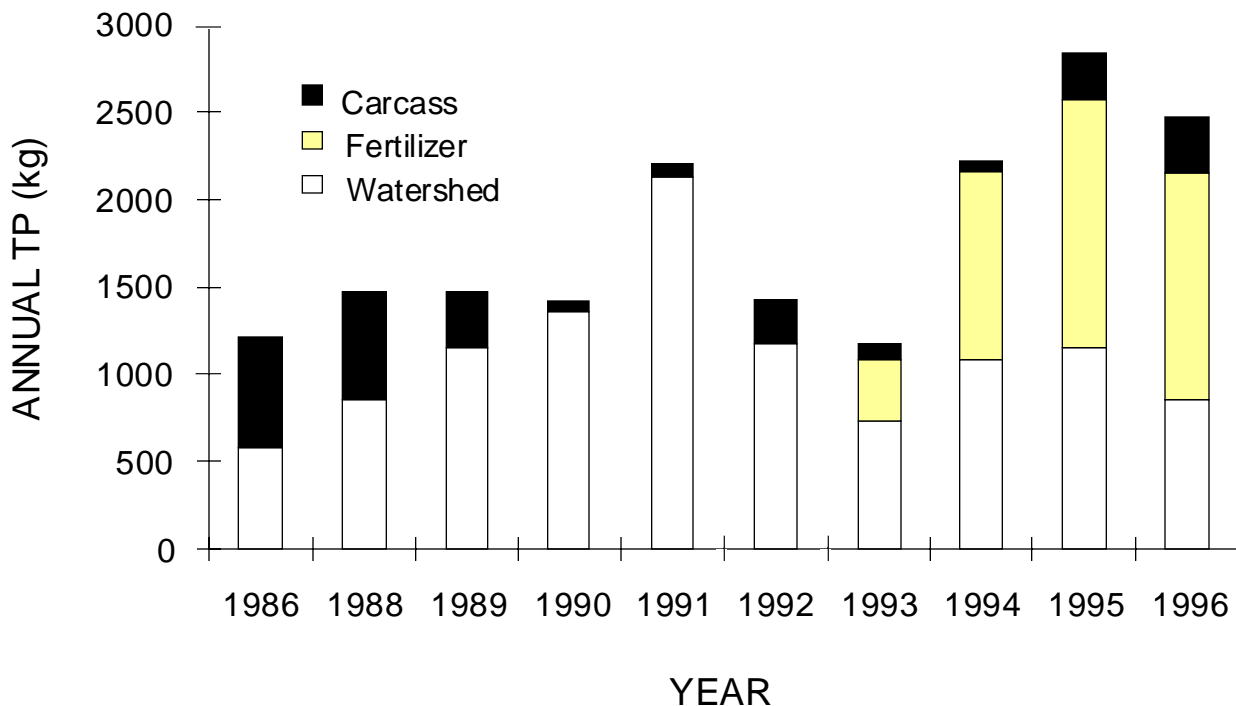

Figure 6. Annual input of total phosphorus (TP) from fish carcasses, fertilizer, and the watershed for Coghill Lake, 1988–1996.
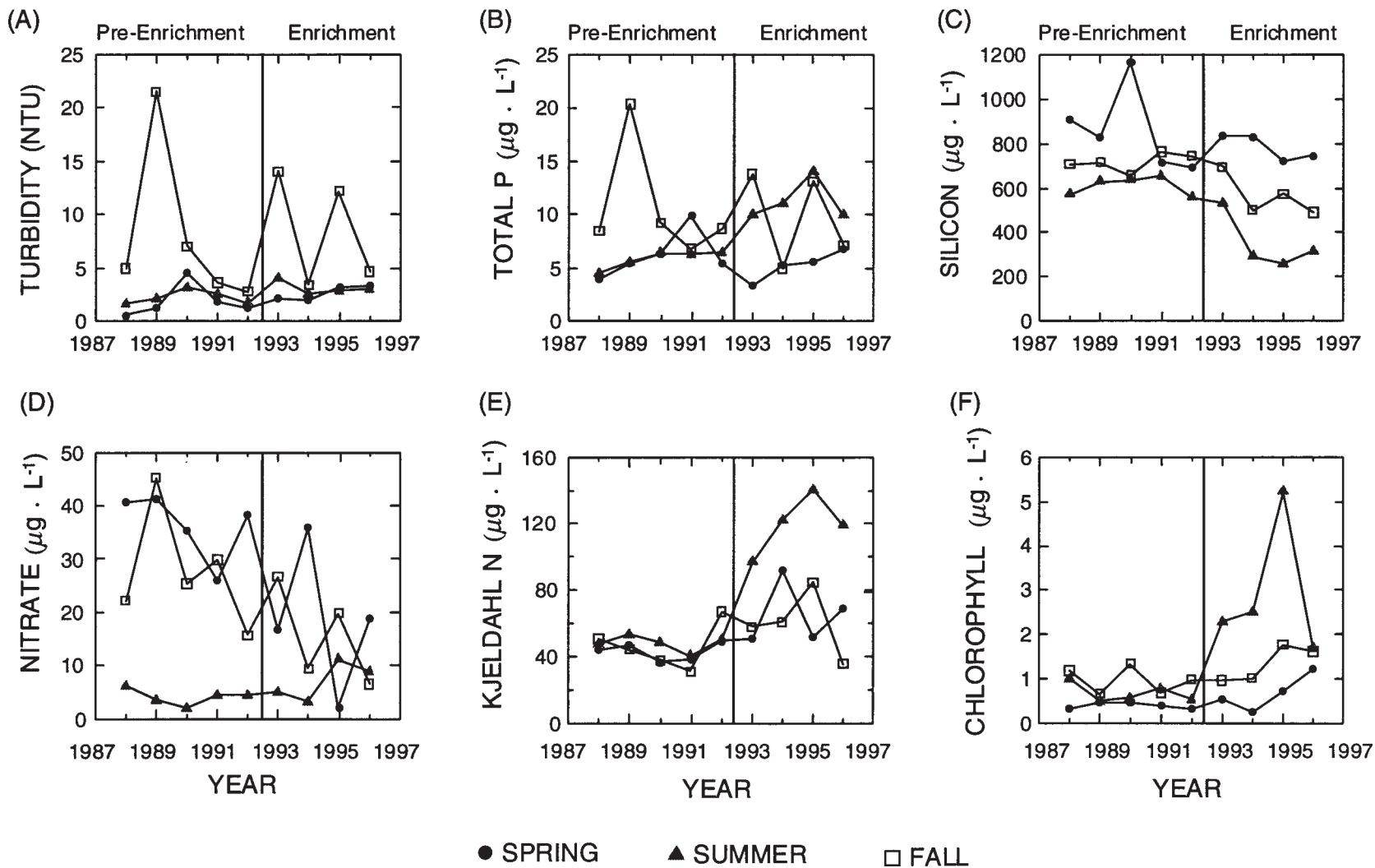
Figure 7. Interaction plot, by season and year, of mean responses for (A) turbidity, (B) total phosphorus, (C) reactive silicon, (D) nitrate, (E) Kjeldahl nitrogen, and (F) chlorophyll-a, 1988–1996.
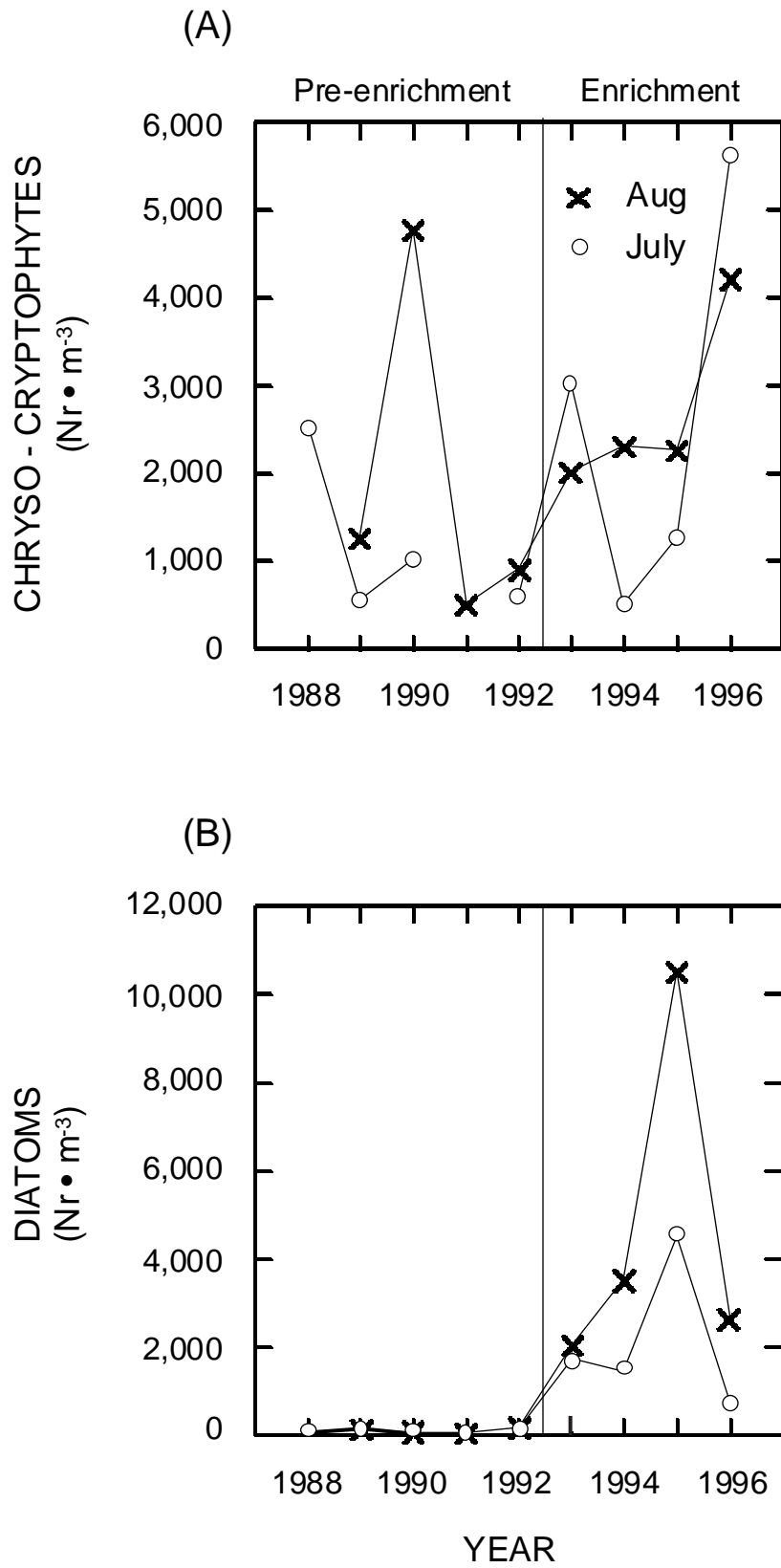
(A)

(B)

Figure 8. Density of (A) chryso-cryptophytes and (B) diatoms during July and August in Coghill Lake, 1988–1996.

Table 3. Results of ANOVA using a randomized block design to test for significant differences ($\alpha = 0.05$) of mean values for zooplankton variables between stations A and B (1988–1996), and between the pre-enrichment (PE; 1988–1992) and enrichment (E; 1993–1996) periods. ANOVA results for the PE and E periods are presented with and without the 1988 data because of probable sample error (*see* Discussion).

Taxa	Station Mean		Approximate Probabilities A vs B	Period Mean (including 1988)		Approximate Probabilities PE vs E	Period Mean (excluding 1988)		Approximate Probabilities PE vs E
	A	B		PE	E		PE	E	
Density (number·m⁻²)									
Cyclops	36,987	51,343	0.045	41,433	47,581	0.343	21,958	47,581	0.007
Bosmina	769	956	0.378	131	1,778	<0.001	131	1,778	<0.001
Body size (mm)									
Cyclops	0.73	0.74	0.645	0.73	0.75	0.374	0.73	0.75	0.268
Bosmina	0.43	0.41	0.406	0.47	0.36	0.071	0.48	0.36	0.017
Biomass (mg·m⁻²)									
Cyclops	69.9	101.0	0.213	73.1	100.8	0.264	47.8	89.8	0.026
Bosmina	1.1	0.9	0.386	0.2	2.0	<0.001	0.3	2.6	<0.001

ible (by herbivorous zooplankton) chryso-cryptophytes appeared higher in the summer (July–August) in 1996, compared to other years, between-year differences were not ($P = 0.151$) statistically different (Figure 8A). Diatoms were the predominant microplankton (20–200 μm), and during enrichment densities reached 10,000·m⁻³, whereas during pre-enrichment densities were consistently <100·m⁻³ (Figure 8B). The summer mean diatom density increased more than 40-fold to 3,362·m⁻³ during enrichment compared to 76·m⁻³ during pre-enrichment; the increase was mainly due to higher densities of edible genera, most notably *Achnanthes* and *Cyclotella*.

Over 95% of the macrozooplankton community in Coghill Lake during pre-enrichment and enrichment were *Cyclops*. *Bosmina* were the most prevalent cladoceran, whereas *Daphnia* and *Chydoridae* were seldom found. The seasonal mean zooplankton density for all years sampled ranged from 7,006 to 119,775·m⁻², and the seasonal mean biomass ranged from 18 to 249 mg·m⁻². Spatial (station) differences in seasonal mean density, body size, and biomass for *Cyclops* or *Bosmina* were not significant (Table 3). Differences in *Cyclops* seasonal mean densities ($P = 0.343$), body size ($P = 0.374$), and biomass ($P = 0.264$) were not significant between the pre-enrichment and enrichment periods (Table 3). However, we questioned

the validity of the 1988 zooplankton data, especially the fall data. We believe that a different net size was used in the fall; this would have affected the density calculations because densities were unusually high (200,000·m⁻²) and exceeded the summer density, which was not the seasonal pattern observed in all other years (Figure 9A). When the 1988 zooplankton data are excluded, *Cyclops* seasonal mean densities during enrichment increased by 117%, from 21,958·m⁻² to 47,581·m⁻², and the biomass nearly doubled from 48 mg·m⁻² to 90 mg·m⁻² (Table 3).

Before enrichment *Bosmina* were very sparse, densities typically <300 animals·m⁻² and the biomass <1 mg·m⁻². However, in the second year of nutrient treatment (1994), *Bosmina* density and biomass increased markedly, and a pronounced peak was observed in the fall (Figure 9B). In the next 2 years of enrichment (1995 and 1996), peak abundance occurred again in the fall, but densities were less than in 1994. Nonetheless, a fall *Bosmina* bloom occurred during the last 3 years of treatment, and a significant increase ($P < 0.001$) in seasonal mean *Bosmina* density and biomass occurred during enrichment (Table 3).

The sockeye salmon smolt population estimate averaged 263,604 for 3 years before enrichment and 940,411 for 3 years during enrichment (Table 4).

(A)

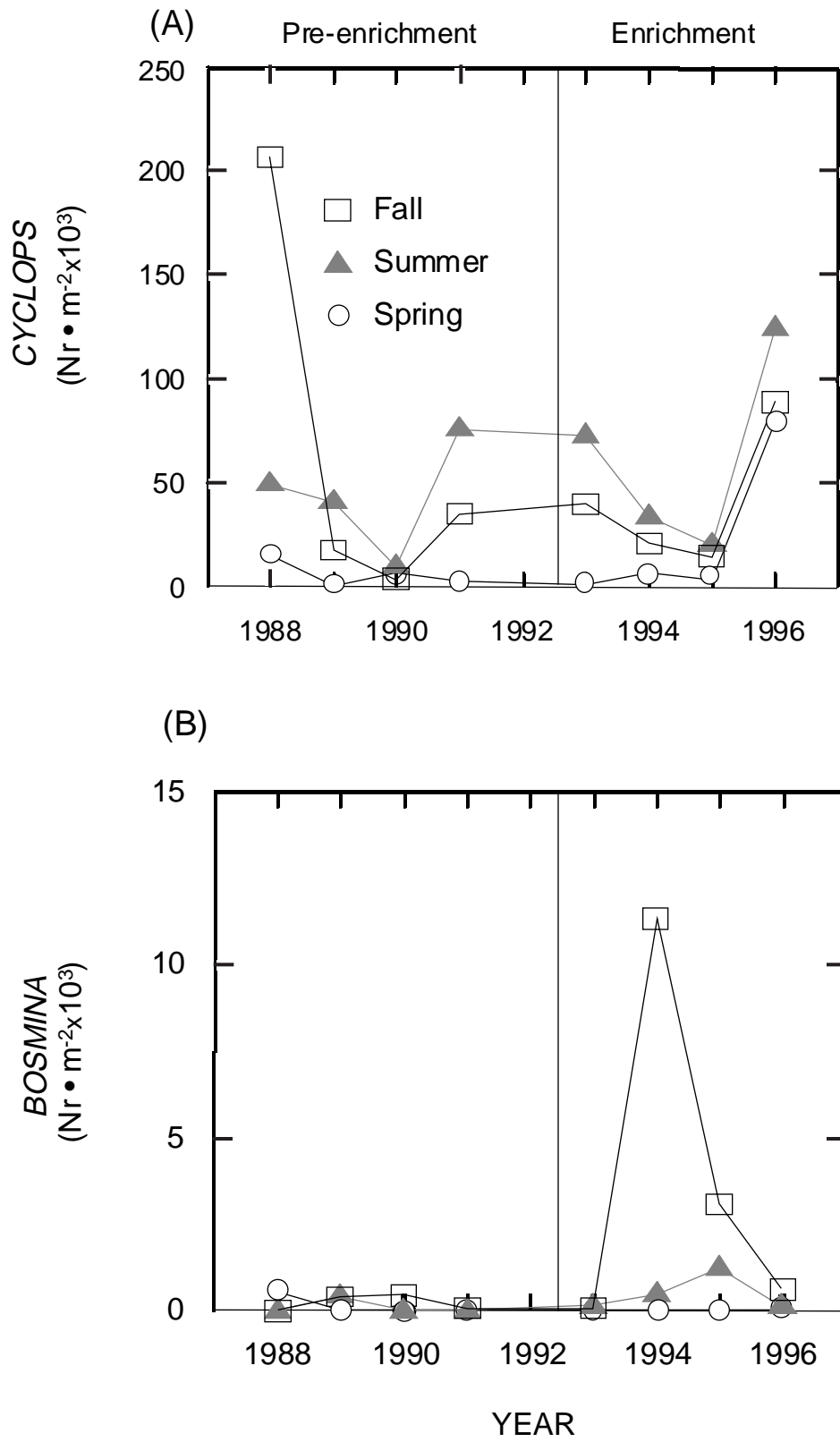Pre-enrichment   Enrichment

(B)

Figure 9. Interaction plot by season and year of mean responses for (A) *Cyclops* and (B) *Bosmina* density, 1988–1996.

Table 4. Yearly total population estimates for Coghill Lake sockeye salmon smolts during pre-enrichment and enrichment periods, and mean smolt estimates for both periods. Also shown are the estimates of age-1 composition and size in 1996 following their stocking as fingerlings in the fall of 1995.

Smolt Year	Total Smolt Population Estimate		Composition		Age-1 Length		Age-1 Weight	
	Nr	SE	(%)	SE	(mm)	SE	(g)	SE
				Pre-enrichment				
1989	373,986	8,642	99.0	0.32	51.8	0.209	1.04	0.015
1991	133,900	21,899	80.2	1.31	60.2	0.332	1.52	0.017
1993	282,925	27,900	94.8	2.14	55.0	0.195	1.83	0.032
Mean	263,604		91.3		55.7		1.46	
				Enrichment				
1994	1,093,575	85,174	97.3	0.59	56.6	0.142	1.39	0.012
1995	1,537,968	127,297	95.9	1.11	59.7	0.279	1.52	0.027
1996								
Wild	189,691	38,544	99.3	1.72	60.8	0.181	1.53	0.015
Hatchery	299,328	59,257	100.0	na	65.2	0.313	2.02	0.032
Mean[a]	940,411		97.5		59.0		1.48	

[a] Mean of 1994 through 1996 excluding 299,328 smolts from 865,000 hatchery-produced fingerlings stocked in Coghill Lake in 1995.

The 1991 smolt emigration was the lowest (133,900) for the 6 years, and the 1995 emigration was the largest (1,538,000). The 1996 smolt emigration was an estimated 489,000, of which 61% (299,300) were produced from the stocking of 865,000 fingerlings in the fall of 1995. Age-1 smolts composed 80.2–99.7% of the total emigration during the 6 years (Table 4). Age-1 smolt lengths and weights averaged about 58 mm and 1.5 g (Table 4), and differences in size between the pre-enrichment and enrichment periods were not significant.

During pre-enrichment, age-1 smolts per spawner ranged from a low of 2 in 1989 (produced by the 1987 brood year, which was the year of the record-high escapement of 187,000), to a high of 29 in 1993 (produced by the 1991 brood year escapement of 9,700; Figure 10). During enrichment the number of smolts per spawner increased to 37 in 1994 and to 167 in 1995, but decreased to 26 in 1996. However, the number of smolts per spawner in 1995 was probably lower because the 1993 escapement was underestimated; i.e., flooding washed out the adult weir before the end of the sockeye run and an unknown but potentially large number of adults subsequently entered the lake (based on aerial survey). However, we believe the number of 1995 smolts per spawner was still greater than in other years.

DISCUSSION

Nutrient enrichment of Coghill Lake resulted in significant decreases for some of the general water chemistry (e.g., conductivity, pH, and alkalinity) measurements; however, these decreases, at 1 or 2 units of measure, were very slight and their effect on biological productivity was small (Table 2). Although higher nutrient (TP and TKN) concentrations, algal biomass, and zooplankton biomass were achieved during enrichment (Tables 2 and 3), the oligotrophic status of Coghill Lake remained unaltered (e.g., seasonal mean TP remained at $<10 \ \mu g \cdot L^{-1}$). These results, in addition to the lower nitrate and silicon concentrations during enrichment (Table 2), indicate increased assimilation by the more numerous phytoplankton (Figure 8) and suggest that enrichment benefited primary and secondary production.

Coghill Lake's meromictic and glacial influences both have a profound effect on the physical environment, nutrient cycling, and plankton community, making it atypical of most sockeye salmon nursery lakes. In contrast to holomictic lakes, in which the entire water column is mixed, meromictic lakes do not undergo complete mixing of the water column (Wetzel 1975). In meromictic lakes, organic material transported to the sediments is not recycled back into the trophogenic zone because the monimolimnion prevents turnover,
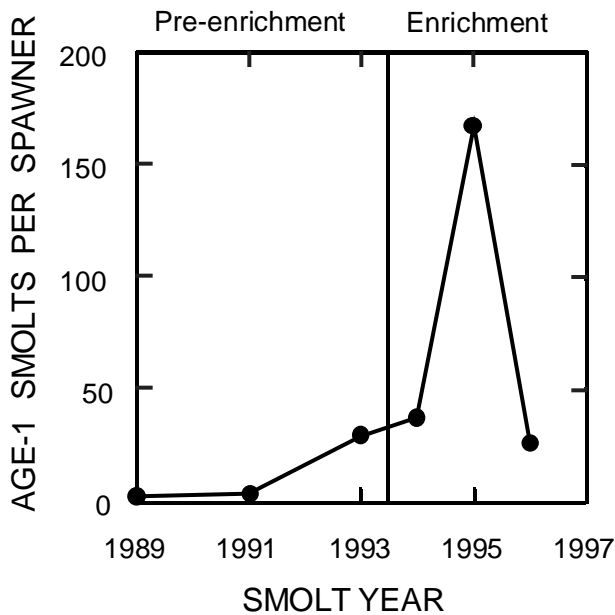
Figure 10. Age-1 sockeye smolts per spawner (i.e., from the parent-year escapement) for Coghill Lake, 1989–1996.

or overall mixing of the water mass. Turnover, however, is not the only mechanism available to supply the mixolimnion with inorganic nutrients. A large portion of the summer production of organic material can be effected via turbulence, which causes particle retention within the mixed layer of temperate lakes (Fee et al. 1994). The strong circulation of the mixolimnion during the summer in Coghill Lake helps to sustain nutrients within the trophogenic zone. In addition, most nutrients in the fertilizer applied to Coghill Lake were inorganic and in a soluble form readily assimilated by phytoplankton. Thus, not all the applied nutrients were quickly lost to the monimolimnion because the seasonal mean TP and TKN concentrations in the mixolimnion increased significantly (Figure 7B and 7E) during the summer, when the lake was fertilized and nutrient incorporation into particulate matter was reflected by the dramatic increase in phytoplankton following enrichment.

Although TP is directly correlated with turbidity derived from inorganic sediments (Hoyer and Jones 1983) and glacial silt (Koenings et al. 1986), during enrichment of Coghill Lake higher TP concentrations could not be attributed to increased glacial runoff because turbidity throughout the 9 sample years was low (<5 NTU) and relatively constant in the spring and summer (Figure 7A). In addition, differences in turbidity between the pre-enrichment and enrichment periods were not significant (Table 2). Hence, the 2-fold increase in summer TP concentration during enrichment (Figure 7B), when turbidity did not increase,

indicates the increase resulted directly from fertilization.

The contribution of salmon carcasses to nutrient loading and effects on lower trophic levels can be important to sockeye salmon production (Donaldson 1967; Mathisen 1972; Stockner 1987). In Karluk Lake, for example, sockeye salmon escapements provide >40% of the annual TP input (Koenings and Burkett 1987b). However, in Coghill Lake the potential nutrient contribution of carcasses from recent (1995–1996) escapements of about 30,000 represents only about 10% of the annual TP input (Figure 6). In contrast, the fertilizer was a major contributor to the nutrient load, composing 40–60% of the annual phosphorus input during the last 3 years of treatment, and hence elevated TP and TKN concentrations (Table 2).

Despite higher nutrient concentrations and algal biomass during the 4 years of treatment, neither *Cyclops* nor *Bosmina* immediately increased in density as expected (Figure 9). Highly enriched conditions (i.e., N:P ratios <18:1) favor production of filamentous or other nonedible phytoplankton too large for zooplankton grazing (Smith 1983; Stockner and Shortreed 1988). However, N:P ratios in Coghill Lake were relatively high (about 40:1) and consistent throughout the 9-year study and were in the range for oligotrophic lakes. In addition, the summer phytoplankton biomass included such taxa as *Achnanthes* and *Cyclotella,* which are considered to be excellent forage for cladocerans (e.g., *Bosmina;* Gliwicz 1975; Berquist et al. 1985). Apparently, the slow response by the zooplankton community to nutrient enrichment was due to factors other than the quality of algal forage.

Cladocerans are not commonly found in glacial lakes because their nonselective filter-feeding strategy is inefficient in the presence of high concentrations of inorganic silt particles, which overlap the size range of edible algae (Koenings et al. 1990). However, *Bosmina* are present in Coghill Lake, though in low abundance (Figure 9B). Unlike most glacial lakes in Alaska, Coghill Lake experiences spring and summer clear-water phases during which turbidity is low (Figure 7A) and light penetration is deep. Under these conditions a greater potential for increased primary productivity exists, and algal food particles can be better exploited by filter feeders.

Collapsed zooplankton populations resulting from heavy grazing pressure by juvenile sockeye salmon can take several years to recover (Kyle et al. 1988; Kyle 1996; Koenings and Kyle 1997). Small cladocerans that have a high reproductive potential, such as *Bosmina*, are often the first to respond to increases in phytoplankton abundance under enriched conditions

(Vanni 1986; Stockner 1987), as was the case in our study. *Bosmina,* which were the first zooplankton to respond to enriched conditions, increased in density during the second year (1994) of treatment and peaked in the fall (Figure 9B). Fry densities were presumably higher in 1993 compared to 1994 because the 1992 escapement (30,000) was 3 times higher than the 1993 escapement (9,000); however, we reject the notion that heavy zooplanktivory during the first year of treatment cropped a *Bosmina* bloom and masked a response to enrichment. *Bosmina* densities were also very low in the 2 years before treatment when sockeye fry densities were also low following small 1990 and 1991 escapements of about 10,000. Instead, we believe excessive grazing was responsible for the depressed zooplankton in Coghill Lake before enrichment (Edmundson et al. 1992) and that ovigerous *Bosmina* were too few in number during the first year of enrichment to show a major increase and provide a major prey item for sockeye fry.

The increase in abundance of *Cyclops* did not track that of *Bosmina* during the enrichment period (Figure 9); *Cyclops* densities did not substantially increase until the fourth year of treatment. Unlike *Bosmina*, which can produce several broods per season, *Cyclops* have a much longer life cycle (Nilssen 1980). In addition, sockeye fry in Coghill Lake are highly selective for ovigerous *Cyclops* (Edmundson et al. 1995). The initial delay in increases of *Cyclops* populations is most likely a result of increased planktivory due to the relatively high fry densities in the lake during 1993 and the high selectivity by sockeye fry. Thus, it is not surprising that heavy grazing by juvenile sockeye salmon, coupled with a protracted reproductive strategy, contributed to the delayed response of *Cyclops* in Coghill Lake, even under enriched lake conditions.

There was little difference in age-1 smolt size between the pre-enrichment and enrichment periods (Table 4). Despite consistently small smolt sizes (Table 4), increases in primary and secondary production apparently resulted in greater freshwater survival and contributed to the 250% increase in smolt abundance. This increase in smolt abundance was not simply due to higher escapements because the number of smolts produced per spawner increased during enrichment (Figure 10). Low smolts per spawner in 1996 relative to 1995 (Figure 10) could have been due to increased competition for food resources from stocking nearly 900,000 relatively large (3.8 g) presmolts in the fall of 1995. However, we believe the effects of stocking on indigenous sockeye fry growth and survival was negligible because stocking occurred in November, when the lake begins to freeze and fry feeding typically ceases. In addition, smolts begin their seaward migration in the spring, when the lake is still ice-covered, so competition for limited food early in the spring also does not explain the lower-than-expected number of smolts produced in 1996.

The mean size of age-1 smolts in Coghill Lake at 1.5 g is considered small and suboptimal for marine survival (Koenings and Burkett 1987a; Koenings et al 1993). However, consistently small smolts, regardless of their natal escapement size, were also observed in meromictic Hugh Smith Lake (Peltz and Koenings 1989), where the narrow range of smolt size before and after nutrient enrichment led to the hypothesis that juvenile sockeye salmon growth was not solely dependent upon the forage base. Instead, growth modeling (Peltz and Koenings 1989) strongly suggested that the small size of smolts in Hugh Smith Lake was controlled by cool rearing temperatures. Stockner (1987) also suggested that differences in epilimnetic temperatures in British Columbia lakes accounted for some of the variation in age-1 sockeye salmon smolt size. Due to the late ice breakup, the input of cold glacial meltwater, and strong wind mixing in Coghill Lake, juvenile salmon growth is probably influenced by suboptimal rearing temperatures and the relatively short growing season (Figure 4).

Increases in primary and secondary productivity in meromictic and glacially influenced Coghill Lake led to enhanced sockeye salmon production similar to that observed in other holomictic and meromictic (clear-water) lakes treated in Alaska (Kyle 1994a, 1994b; Kyle et al. 1997). Although nutrient enrichment increased lake productivity and smolt production in Coghill Lake, a balance between fry densities and the existing forage base must be achieved to prevent overgrazing and attendant long-term impacts on the juvenile sockeye forage base.

Finally, the ultimate benefit and success of the nutrient treatment program would be increased adult returns. This will not be manifest for a few years because the first major age class (age 1.3) of adults that, as fry, reared in the lake during enrichment will return to spawn in 1997. If data on this and subsequent returns become available, analyses will be attempted. However, whether adult production increased, decreased, or remained static due to fertilization may be difficult to separate from potential climate changes and variable oceanic conditions that strongly influence marine survival (Plante and Downing 1993; Hinch et al. 1995). Nevertheless, an index to the magnitude of oceanic survival effects should be extractable by examining escapements in nearby untreated stocks.

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